National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Reprinted from

Canadian Journal of Forest Research

Réimpression de la

Revue canadienne de recherche forestière

Variable-quality form in mature jack pine stands: quantification and relationship with environmental factors

DAVE M. MORRIS AND WILLIAM H. PARKER

Volume 22 • Number 3 • 1992

Pages 279–289

Printed in Canada / Imprimé au Canada

Variable-quality form in mature jack pine stands: quantification and relationship with environmental factors

DAVE M. MORRIS

Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Centre for Northern Forest Ecosystem Research, c/o Lakehead University, Thunder Bay, Ont., Canada P7B 5E1

AND

WILLIAM H. PARKER

School of Forestry, Lakehead University, Thunder Bay, Ont., Canada P7B 5E1

Received January 16, 1991

Accepted September 16, 1991

MORRIS, D.M., and PARKER, W.H. 1992. Variable-quality form in mature jack pine stands: quantification and relationship with environmental factors. Can. J. For. Res. **22**: 279–289.

The purpose of this study was to determine quantitatively to what extent various stem, crown, and branching attributes conformed to subjective evaluations of form for jack pine (*Pinus banksiana* Lamb.) in northwestern Ontario and which environmental variables were associated with the form-related variation. Six fire-origin stands established on deep soils were selected on the basis of their form and subjectively evaluated as good (2), medium (2), or poor quality (2). Ten dominant trees were randomly chosen from each stand, and 26 attributes were determined for each sampled tree. These attributes were categorized as growth (2), stem form (6), crown form (6), or branch characters (12). Data on surrounding stand conditions and microsite were also collected. Climatic factors for each stand were interpolated from nearby weather station data. These data were analyzed by canonical discriminant analysis. The first function separated the poor-quality stands from the other two classes, while the second function separated the average- from the good-quality stands. Important variables in the first canonical function were related to stem and crown characters, whereas branch characters were also important in the second canonical function. First and second canonical discriminant axis scores were used as two new summary variables representing quantified estimates of jack pine form and were regressed against environmental data. While competition and spacing variables explained much of the observed variation, climatic and soil moisture variables were also important. From the present results it is unclear whether these variables affect form directly or indirectly by modifying competition and spacing variables over the course of stand development.

MORRIS, D.M., et PARKER, W.H. 1992. Variable-quality form in mature jack pine stands: quantification and relationship with environmental factors. Can. J. For. Res. **22** : 279–289.

L'objet de l'étude est de déterminer à quel point les différentes caractéristiques de la tige, de la cime et des branches sont conformes aux évaluations qualitatives de la forme du pin gris (*Pinus banksiana* Lamb.) dans le nord-ouest de l'Ontario. Une étude des variables environnementales associées aux variations de la forme a aussi été effectuée. Six peuplements d'origine de feu établis sur des sols profonds ont été choisis en fonction de la forme des arbres, qui a été évaluée subjectivement comme étant bonne (2), moyenne (2) ou de mauvaise qualité (2). Dix arbres dominants ont été choisis au hasard dans chaque peuplement et 26 caractéristiques sont mesurées sur chaque arbre échantillon. Les caractéristiques liées à la croissance (2), la forme de la tige (6), la forme de la cime (6) ou la ramification (12) ont été regroupées en catégories. Des données sur les conditions générales des peuplements et des micro-sites ont aussi été notées. Les facteurs climatiques de chaque peuplement sont interpolés à partir des données de la station météo la plus près. Ces données sont analysées par analyse discriminante canonique. La première fonction sépare les peuplements de mauvaise qualité des deux autres classes, alors que la deuxième fonction sépare la moyenne des peuplements de bonne qualité. Les variables importantes dans la première fonction canonique sont liées aux caractéristiques de la tige et de la cime, alors que les caractéristiques de ramification sont importantes dans la seconde fonction canonique. Les valeurs des deux premières composantes canoniques ont été considérées comme deux nouvelles variables de synthèse représentant des estimations quantifiées de la forme du pin gris. Des régressions entre ces variables de synthèse et les données environnementales ont également été produites. Les variables de compétition et d'espacement expliquent le mieux la variation observée, toutefois les variables climatiques et de l'humidité du sol sont importantes. À partir de ces résultats, il ne semble pas que ces variables affectent la forme directement ou indirectement, par une modification des variables de compétition et d'espacement sur la direction du développement du peuplement.

[Traduit par la rédaction]

Introduction

Jack pine (*Pinus banksiana* Lamb.) is one of the most conspicuous species in Canada's Boreal Forest. Characteristically, it is found in extensive pure stands established after wildfires or in mixtures with black spruce (*Picea mariana* (Mill.) B.S.P.). Jack pine also occurs as a component of various mixed conifer–hardwood associations (Whitney and McClain 1981; Kenkel 1986). Usually it grows on dry, sandy soils, but this species also grows on a large variety of deep to shallow soils (Fowells 1965).

Jack pine is second only to black spruce as the most important species harvested in Ontario, constituting 34.3% by volume of the total conifer cut (Ontario Ministry of Natural Resources 1990). Presently in northwestern Ontario, both the lumber and pulping industries utilize the species. A common belief among foresters is that while poor-form trees are unacceptable for lumber production, they are still suitable for pulping. Unfortunately, poor-form trees are desirable neither for lumber nor pulp, as they produce unstable structural lumber or low yields of poor-quality pulp (Timell 1986; Zobel

Printed in Canada / Imprimé au Canada

92-06105/

and van Buijtenen 1989). In this context, quality is determined by the criteria of stem straightness, branch size, branch angle, and number of knots present along the tree bole. Since more than 60% of the land artificially regenerated annually in Ontario is planted or seeded with jack pine (Ontario Ministry of Natural Resources 1987), a definite need exists to establish and grow forest stands with desirable stem qualities. Unfortunately, many unanswered questions remain concerning what factors and (or) processes determine stem quality.

Jack pine is one of Ontario's most variable species in terms of growth and, especially, form characters (Hosie 1969). It is generally accepted that genetics can make an important contribution to form (Rudolph and Yeatman 1982; Ontario Ministry of Natural Resources 1987). This contention is based primarily on research results for other tree species demonstrating that the various attributes that contribute to form such as branch angle, stem straightness, and limbiness are under fairly strong genetic control (Magnussen and Yeatman 1987). Presumably, this relationship will also prove to be the case for jack pine. Furthermore, it has been hypothesized that localized genetic differences may be present in this species for two reasons. First, the species is thought to have a limited effective pollination distance; and second, its seed dispersal potential is spatially and temporally restricted in the Boreal Forest owing to its production of serotinous cones in this forest region (Morgenstern *et al.* 1975).

Interacting with this genetic control of form characters, other environmental conditions have been recognized as factors contributing to form (Zimmermann and Brown 1971). Site quality can be an overriding factor in determining form in jack pine. On the poorest bedrock sites with little soil, the trees are short and deformed with twisted widespreading branches (Hosie 1969). On more fertile sites with deeper soils, stocking becomes a more important determining factor. Open-grown wolf trees have limby open crowns with branches arching upwards from tapered boles. Trees from closed-canopy stands have receding, greatly reduced live crowns and slender trunks with little taper. Although total volume of wood (including branches) produced in stands grown to maturity is not influenced by initial spacing, except at the extremities of the density range (law of constant final yield; Harper 1977), the least dense stands produce low harvestable stem yields per unit area.

While spacing affects form of jack pine, the factors that determine spacing in mature natural stands are complex. This complexity depends, to a large degree, upon seed-source availability, as well as on a host of environmental and competition factors, which in turn, affect levels of mortality and stand development (Kenkel 1988). The destruction by fire of a densely stocked mature stand leads to a replacement stand with a very high initial density, but which also has a mortality rate that increases linearly with stand age over much of its history owing to intraspecific competition (Yarranton and Yarranton 1975).

Forestry practices can do little to improve jack pine growth and form on the poorest sites, but silvicultural and tree improvement techniques can help assure good form on higher quality sites. While it is known that spacing and intraspecific competition play major roles in the resulting tree form (Bella and De Franceschi 1974, 1980), it has not yet been determined what initial spacing(s) will optimize tree form in plantations. Still, the trend today is to plant at spacings wider than the traditional 2 m in northern Ontario, with 3-m spacing advocated by some to reduce costs. Concern exists that these initial spacings may be too wide and negatively affect tree form and hence the value of the resulting stand. Janas and Brand (1988) compared the growth and development of 21-year-old plantations established at different spacings (2.13 × 2.13 m and 4.27 × 4.27 m) to natural stands of similar age. They reported that stem quality was better in the natural stands than in the two plantations. Trees grown at close spacing had slightly better stem quality (defects present but located farther up the bole) than those grown at wide spacing. Their stem quality classes were based, collectively, on the number and location of crooks, presence and location of forks, degree of sweep, and branch diameter.

In practice, the assessment of form in jack pine is a subjective decision based on an overall evaluation of several key variables. Some of these variables are inherently quantitative (e.g., branch angle, branch diameter, branch length, crown recession rate); some are qualitative (e.g., presence of crooks); and some can be expressed either way (e.g., limbiness, sweep). Because of the direct bearing of these traits on the value of jack pine stands to the forest industry, improvement of these attributes is an important goal in forestry. Before this goal can be met by either silvicultural or tree improvement procedures, answers are needed to several basic questions: (*i*) Which of these attributes are most important in determining form, and hence the value of harvested trees? (*ii*) To what extent are these attributes correlated with each other? (*iii*) Do interactions exist between the attributes? (*iv*) What is the relative importance of the various environmental forces including spacing in determining these traits? (*v*) To what extent does genetics determine each of these attributes? (*vi*) Does genetics make an equally important contribution in determining these form traits in varied environmental settings? While these questions cannot be fully answered without field trials and progeny testing, systematic investigation of the form of individuals within natural stands differing in overall quality and the environmental circumstances associated with this form can help provide additional understanding of the factors and processes involved.

Our goals in this study were to compare natural stands of jack pine from northern Ontario that had been subjectively evaluated by forest management experts on the basis of overall stand quality. We wished to determine in a quantitative manner to what extent the various attributes confirmed the subjective evaluations. We also wished to investigate how much of the variation in stand quality could be explained by various environmental variables.

Materials and methods

Stands and collections

During the summer of 1989, six fire-origin stands of jack pine with variable tree form were identified for collection of representative sample trees from the North Central Region of Ontario. Since relatively steep clines had been shown to exist for several morphological features of jack pine in the area of Lake Nipigon (Schoenike 1976; Rudolph and Yeatman 1982; Maley 1990), three stands were chosen to represent the area east of the lake (stands 11, 12, and 13) and three were chosen to represent the area west of the lake (stands 21, 22, and 23). The locations of these six stands are illustrated in Fig. 1. Forest management experts from each area were asked to identify a stand having the best possible quality, a stand having poor quality,

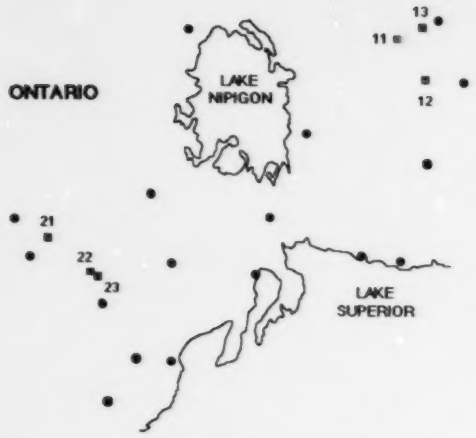

FIG. 1. A sketch of northwestern Ontario identifying the six stand locations (squares) and 17 of 27 weather stations (circles) included in the map coverage.

and a stand having average quality. This quality judgement was based on an overall assessment of stem, crown, and branching attributes. Both of the best quality stands (11 and 21) had previously been used to provide plus trees for Ontario Ministry of Natural Resources' and Ontario Tree Improvement Council's selection programs.

Only stands growing on deep soils (>100 cm) were selected, thus eliminating from consideration poor-quality stands growing on shallow soils over bedrock. Initially, an attempt was made to choose stands of the same age and average height to minimize the effects of size and developmental differences in comparisons based on form variables. This attempt proved impractical, and the six chosen stands showed considerable variation in their average values for most mensurational parameters: age, 48–107 years; average height, 15–23 m; diameter at breast height, 15–29 cm; stand density, 463–2513 stems/ha; and total basal area, 15.6–29.4 $m^2 \cdot ha^{-1}$ (Table 1). The two good-quality stands (11 and 21) were essentially pure jack pine stands; the average-quality stands (12 and 22) each contained 20% black spruce; and the poor-quality stands (13 and 23) contained 30 and 10% black spruce, respectively.

Ten dominant jack pine trees were randomly chosen from each of the six stands using a Cartesian coordinate system. Three constraints were added to the tree selections: (*i*) chosen trees had to be separated by a minimum of 100 m to ensure sampling of different families; (*ii*) chosen trees had to bear at least 20 closed seed cones to provide the basis for further progeny tests; and (*iii*) chosen trees had to be at least 30 m from permanent roads to eliminate the influence of this human disturbance on crown development.

Data collection

The 60 selected trees were felled, and a series of measurements were made to quantify both growth and form characters. Total heights and diameters at breast height were measured, and basal ages were determined.

Tree form characters fall broadly into stem, crown, or branch categories. Stem variables measured included (*i*) degree of sweep from the perpendicular measured as the angle of deviation from vertical (before felling), (*ii*) distance from the tree base to the start of the bole sweep, (*iii*) number of major crooks in the stem, (*iv*) distance from the tree base to the first crook, (*v*) stem taper, and (*vi*) shape of taper. Taper is defined as the change in stem radius divided by the length of the bole between the two radial measurements (Forslund 1991), and shape defines the bole profile curve (Forslund 1991). A shape value of 2 represents a parabola, whereas a value of 1 represents a cone.

Crown form was quantified by measuring (*i*) crown length, (*ii*) crown diameter sampled at 2, 4, and 6 m from the tree's apex, (*iii*) crown density as a percent of total crown volume occupied by foliage, and (*iv*) crown recession rate. To obtain the crown recession rate, three discs, each encompassing a whorl of dead branches, were cut approximately 2, 4, and 6 m below the base of the live crown. The distance from the base of the live crown to each branch stub was measured and tallied. Following the methodology decribed by Maguire and Hann (1988), cross-sectional cuts through three major branch stubs per disc were made with a band saw in the laboratory to expose longitudinal sections through the branch stubs. The number of discontinuous rings between the branch stub and the bole corresponds to the number of years the branch has been dead. By dividing the number of years dead into the actual distance between the branch stub location and the base of the live crown, a crown recession rate (m/year) was obtained.

Measurements of branch characters included the number of live branches per metre sampled at 2, 4, and 6 m from the tree's apex, as well as branch lengths, diameters, and angles for four branches at each of these three locations.

Four separate measures of the level of competition imposed upon each sampled tree by the surrounding stand were obtained. The first measure of competition was stand density (stems/ha) computed from an average intertree distance for each stand. The second measure of competition was a simple basal area sweep, using a 2 $m^2 \cdot ha^{-1}$ prism, taken from the centre of each sampled tree's stump. The third competition measure attempted to quantify both the horizontal (between-tree distances) and vertical (crown volumes) influence of the first-order competitors within each quadrant surrounding the sample tree. For each of the four competitors, total height, crown length, crown width, crown density, and distance to each subject tree were obtained. Crown volumes were then computed for each of the competitors. A competition index was then computed for each sampled tree by summing the four competitor crown volumes after being divided by the squared distance between the competitor and the subject tree. The final competition measure attempted to quantify the total available growing space each sampled tree could utilize. Vertical hemispherical photographs, using a 35-mm reflex camera and a 7.5-mm fish-eye lens, were taken directly over the sampled tree's stump at a standard height of 1 m. The percent of open canopy was measured using a planimeter on the resulting photographs.

Microsite attributes were measured from soil pits dug to a depth of 1 m located in close proximity to each of the sampled trees. The site conditions were evaluated according to the soil sampling guide from the Forest Ecosystem Classification system for the North Cental Region of Ontario (Ontario Institute of Pedology 1985). The measurements obtained included (*i*) depths of LFH, A, B, BC (if present) horizons, (*ii*) field textures of each horizon, (*iii*) percent of coarse fragments within each horizon, (*iv*) soil moisture index, (*v*) soil drainage index, and (*vi*) aspect and degree of slope.

Six climatic variables (frost-free days, average January temperature, average July temperature, annual total snowfall, annual total precipitation, growing degree-days) were interpolated for each of the six stands using the TIN (triangulated irregular network) subpackage of ARC/INFO software (Environmental Systems Research Institute 1987) running on a Prime minicomputer at the Centre for the Application of Resource Information Systems at Lakehead University. Two steps were involved in this procedure. First, climatic data for 30 years (1951–1980), obtained from 27 Canadian weather stations blanketing the stand locations (Environment Canada 1982*a*, 1982*b*), were used to produce trend surface models for each of the six variables. Interpolated stand values for each variable were then determined directly from the models following entry of geographic coordinates and elevation of the stands.

Data analysis

A series of one-way ANOVA were performed on each of the measured variables to determine the importance of these variables, independent of each other, in determining stand quality. Of these variables, 13 varied directly with the size of the individual tree. Since

TABLE 1. Means and summary data for good-, average-, and poor-quality stands of jack pine

	Stand classification[a]					
	Good		Average		Poor	
	21(W)	11(E)	22(W)	12(E)	23(W)	13(E)
Site data						
Lat. (N)	49°09′	50°07′	48°56′	49°52′	48°54′	50°10′
Long. (W)	90°17′	87°04′	89°57′	86°52′	89°53′	86°50′
Elev. (m asl)[b]	495	335	510	365	510	320
Summary data						
Height (m)	20.2	22.6	19.2	21.5	18.3	15.1
	(0.93)	(1.20)	(1.58)	(1.79)	(1.59)	(1.21)
Age (years)	78.1	107.3	59.7	80.6	61.4	48.3
	(0.88)	(3.92)	(12.9)	(26.7)	(8.74)	(2.95)
DBH (cm)	23.4	25.4	23.1	21.4	28.5	14.6
	(2.61)	(3.05)	(3.56)	(4.10)	(5.30)	(3.12)
Competition data						
Density (stems/ha)	1242	819	635	1499	463	2513
	(575)	(260)	(244)	(725)	(176)	(1257)
Total basal area ($m^2 \cdot ha^{-1}$)	27.4	28.4	18.8	29.4	15.6	16.5
	(6.47)	(8.10)	(3.29)	(4.21)	(4.20)	(5.23)
Competition index	4.77	7.44	10.41	10.03	9.52	4.07
	(2.54)	(2.53)	(5.22)	(6.26)	(4.52)	(2.50)
% opening	4.64	5.38	5.89	2.85	7.88	2.90
	(1.44)	(1.28)	(2.21)	(1.42)	(2.89)	(1.26)
Microsite data						
Depth LFH (cm)	12.1	10.0	11.1	9.1	6.8	9.4
	(4.04)	(3.37)	(1.91)	(3.11)	(2.53)	(2.99)
Depth A (cm)	5.7	6.6	4.0	8.7	2.9	7.2
	(2.79)	(2.01)	(2.31)	(3.71)	(1.20)	(2.90)
Depth B (cm)	19.2	14.7	16.9	15.2	16.7	29.4
	(5.59)	(3.77)	(10.57)	(4.47)	(4.40)	(11.57)
Depth BC (cm)	14.8	13.4	13.6	10.8	10.3	8.7
	(10.99)	(12.29)	(4.99)	(10.11)	(7.42)	(9.97)
Coarse A (%)	5.0	1.0	1.0	2.0	1.0	1.0
	(7.07)	(3.16)	(3.16)	(4.22)	(3.16)	(3.16)
Coarse B (%)	12.5	8.0	12.0	10.0	3.0	3.0
	(23.00)	(18.59)	(13.17)	(8.16)	(4.83)	(4.83)
Coarse BC (%)	1.0	1.0	18.0	5.0	12.0	5.5
	(3.16)	(9.19)	(16.02)	(6.67)	(24.40)	(6.85)
Coarse C (%)	28.5	20.0	28.5	25.5	34.5	19.5
	(28.68)	(16.83)	(17.33)	(21.53)	(32.01)	(13.01)
Soil moisture index	0.3	0.0	2.0	1.1	1.6	1.0
	(0.67)	(0.00)	(0.00)	(0.57)	(0.97)	(0.82)
Soil drainage index	1.9	1.8	3.0	1.6	2.4	2.2
	(0.57)	(0.42)	(0.00)	(0.70)	(0.70)	(0.42)
Slope (%)	0.3	0.2	0.0	0.2	1.2	0.0
	(0.48)	(0.63)	(0.00)	(0.63)	(1.32)	(0.00)
Climate						
Frost-free days	76.8	72.0	32.4	65.0	26.5	73.4
Jan. temp. (°C)	−25.6	−26.3	−25.6	−27.2	−25.6	−26.0
July temp. (°C)	23.5	23.0	23.8	23.4	23.9	22.9
Precipitation						
Snow (cm)	238	293	219	277	217	290
Total (mm)	797	803	767	807	760	808
Growing degree-days	1324	1173	1232	1263	1221	1167

[a] Values in parentheses represent 1 SD.
[b] asl, Above mean sea level.

we were interested in form differences between stands independent of size, a transformation was required. Therefore, the affected variables were analyzed as studentized residuals of their regressions on tree height and are identified with an "R" in Table 2. This transformation removed the size effect present in our stands that differed in age. This procedure is preferable to standardizing by calculating a simple ratio of each target variable to height, since the transformed data remain normally distributed, which is not the case for ratio-transformed data (Atchley *et al.* 1976). Since planned comparisons were to be made, least significant difference was chosen (Sokal and Rohlf 1981) to identify significant differences between the three stand quality classes.

Using canonical discriminant analysis, a multivariate approach to quantifying tree form was carried out. This procedure identified those measured variables that provided the greatest degree of separation between the three stand quality classes. Reclassification of the individuals into the three quality classes provided an estimate of the accuracy of the derived discriminant function.

Simple linear regressions between the first two canonical functions (dependent variables) derived from the discriminant analyses and the environmental variables (independent variables) were calculated (58 df). The coefficients of determination from the regressions indicated the amount of variation in stand form explained by each of the environmental variables. Multiple linear regression (backward elimination) was used to identify the total amount of variation in stand form explainable by a linear function based on a combination of the environmental factors. The six climatic variables and elevation were obtained on a stand basis (10 trees from each stand had the same value) and therefore were not included in the multiple linear regressions.

Results

The untransformed stand means and standard deviations for the 24 variables determined for this study are presented in Table 2. If the selected variables represent appropriate descriptors of these six stands, then increasing or decreasing trends should be evident for good-, average-, and poor-quality stands. Generally these trends are evident, but exceptions are numerous, particularly where one of the two stands in a poor- or average-quality category has an anomalous value. In terms of stem traits, the average stand from east of Lake Nipigon (12) has values for sweep distance, number of crooks, distance to the first crook, and taper that are comparable to those of the two superior stands. Stand 12 also has a value for crown density that is comparable to that of the good stands. Additional irregularities in the trends from good to poor are evident for the other crown variables, except for crown recession rate, which shows a smooth trend. However, it should be kept in mind that many of these anomalies exist owing to the different sizes of the trees in the six stands and the untransformed nature of the data. For example, the eastern stand exhibiting poor quality (13) has the smallest value for crown length, a variable indicative of crown compactness. A check of the height data for stands (Table 1) reveals that this stand is also the shortest; thus, there is a need for standardization according to height prior to direct stand comparisons for size-related variables.

Univariate ANOVA

Univariate ANOVA was performed on the basis of three quality classes, with eastern and western stand pairs lumped together within the three classes (20 trees per class). Of the 24 variables measured for this study, 13 were transformed to remove the effects of height. Significant differences were present between groups ($p > 0.05$) for half of the selected variables: 3 of the 6 stem variables, 3 of the 6 crown variables, and 6 of the 12 branch variables. For the six stem variables, highly significant differences ($p < 0.01$) were observed between number of crooks, stem taper, and stem shape, while no significant differences were observed for distance to the first crook, sweep, and distance to the sweep. For two of the three significant stem variables (number of crooks and taper), good and average stands form a group distinct from the poor-quality stands (Table 2), indicating that the poor stands are more distinct from average stands than are the superior stands. The third significant variable (shape) indicated a more gradual trend from good to poor, by grouping good with average and average with poor. Although the raw data (Table 2) indicate obvious trends according to stand quality for the two sweep variables, apparently the ranges of variation overlap to such an extent that the differences are not significant.

While significant differences in stand quality were present for three of six crown variables, only two of these, crown density and crown recession rate, seem to be good descriptors of form in this instance. As before, the poor stands formed a group distinct from good and average stands in terms of their crown density. On the other hand, all three stand quality types were clearly distinguished on the basis of crown recession rate (Table 2). This variable was the only one of the 24 that demonstrated the presence of three significantly different groups. While ANOVA of crown-length data demonstrated quality differences among the three groups, the trend was unexpected, with the difference expressed between the good and average stands. This result, coupled with the lack of difference for any of the three crown-diameter variables, suggests that the jack pine stands sampled for this study were relatively homogeneous in terms of overall crown form regardless of their stand quality assessment. This result is unexpected owing to the well-defined crown recession rate results and the considerable variation commonly observed in jack pine crowns in northern Ontario, and it is not clear at this point whether these results may represent a sampling anomaly.

In terms of branch variables, the good-quality stands had significantly fewer branches per metre at the lowest measuring point than average and poor stands (Table 2). This trend did not hold for middle and upper locations, with the average-quality stands having significantly fewer branches than the other two stand classes at the uppermost location and no significant differences present at the midlocation. All three branch-length characters showed no significant differences between quality classes. This result was consistent with the crown-diameter results.

Of the remaining six branch diameter and angle variables, four showed significant differences between quality classes (Table 2). For three of these variables (lower branch diameter, middle branch diameter, middle branch angle) the average-quality stands had smaller branch diameters and greater branch angles. The good-quality stands were placed between the average- and poor-quality stands. A gradual trend from good to poor was indicated for lower branch angle. At the uppermost sampling point, significant differences were not present in branch diameter and angle.

Canonical discriminant analysis

All 24 measured variables were included in a canonical discriminant analysis. This analysis combined all the variables to produce two uncorrelated discriminant functions that provided the maximum separation possible between the three quality classes. Separation of the poor-quality stands from the better quality classes occurred on the first canonical axis (Fig. 2). Separation of the good and average stands occurred primarily on the second canonical axis. Table 3 summarizes the standardized canonical function coefficients for the two canonical functions. These standardized coefficients can be viewed as weighting factors and generally indicate the relative importance of each variable in the derived functions. In looking at the six stem variables, only the number of crooks and stem taper have coefficients greater than 0.900 in the first canonical function. Although the sign is reversed, only taper

TABLE 2. Means and significant differences of form variables measured for good-, average-, and poor-quality stands of jack pine

Variable[a]	Stand classification[b] Good 21(W)	Good 11(E)	Average 22(W)	Average 12(E)	Poor 23(W)	Poor 13(E)	Significant difference[c] (groups)
Stem variables							
Sweep (degrees)	3.80	4.40	4.50	5.10	6.40	7.00	ns (R)
	(3.22)	(2.17)	(2.64)	(3.73)	(3.41)	(4.74)	
DisSwp (m)	6.19	7.31	5.43	9.24	3.69	3.26	ns (R)
	(1.61)	(7.09)	(5.73)	(5.88)	(2.08)	(2.27)	
Crooks (no.)	0.13	0.08	0.16	0.09	0.34	0.46	0.000
	(0.08)	(0.07)	(0.08)	(0.09)	(0.11)	(0.28)	(1, 2) (3)
DisCrk1 (m)	8.34	12.40	4.69	11.00	3.08	3.15	ns (R)
	(5.22)	(9.20)	(2.48)	(6.63)	(1.25)	(1.96)	
Taper (mm/m)	3.74	3.65	4.20	3.41	6.19	3.66	0.003
	(0.51)	(0.54)	(0.63)	(0.31)	(0.18)	(0.71)	(1, 2) (3)
Shape	2.21	2.18	1.94	2.05	1.77	1.89	0.007
	(0.20)	(0.33)	(0.30)	(0.23)	(0.65)	(0.23)	(1, 2) (2, 3)
Crown variables							
CrnLen (m)	7.84	7.74	9.71	8.42	9.00	6.46	0.035 (R)
	(1.17)	(1.63)	(2.35)	(1.59)	(1.05)	(1.42)	(1, 3) (2, 3)
LCrnDia (m)	2.52	2.23	3.00	1.94	4.06	1.76	ns (R)
	(1.00)	(0.44)	(0.89)	(0.62)	(1.22)	(0.72)	
MCrnDia (m)	2.87	2.46	2.86	2.10	3.65	1.72	ns (R)
	(0.82)	(0.52)	(0.62)	(0.59)	(1.11)	(0.51)	
UCrnDia (m)	2.02	2.01	1.86	1.62	2.30	1.34	ns (R)
	(0.57)	(0.59)	(0.74)	(0.46)	(0.88)	(0.39)	
CrnDens (%)	74.0	72.0	69.5	77.0	55.0	62.0	0.001
	(7.0)	(10.9)	(7.6)	(9.2)	(17.5)	(19.7)	(1, 2) (3)
CrnRR (m/year)	0.113	0.074	0.161	0.132	0.189	0.213	0.000
	(0.018)	(0.014)	(0.056)	(0.045)	(0.071)	(0.043)	(1) (2) (3)
Branch variables							
LBrnNum (no./m)	7.7	5.7	10.6	8.3	7.0	11.2	0.033
	(2.95)	(2.54)	(3.24)	(4.06)	(2.79)	(3.65)	(1) (2, 3)
MBrnNum (no./m)	15.1	12.5	15.6	16.5	12.5	14.6	ns
	(4.38)	(3.66)	(4.38)	(3.98)	(3.75)	(3.41)	
UBrnNum (no./m)	18.5	22.0	22.8	24.8	16.5	19.3	0.001
	(3.63)	(4.97)	(6.20)	(5.71)	(3.98)	(3.65)	(1–3) (2)
LBrnLen (m)	1.82	1.51	1.78	1.43	2.56	1.25	ns (R)
	(0.45)	(0.39)	(0.40)	(0.55)	(0.49)	(0.40)	
MBrnLen (m)	1.66	1.54	1.51	1.26	2.16	1.11	ns (R)
	(0.43)	(0.30)	(0.37)	(0.36)	(0.57)	(0.34)	
UBrnLen (m)	1.16	1.05	1.01	0.96	1.31	0.75	ns (R)
	(0.26)	(0.34)	(0.22)	(0.37)	(0.41)	(0.26)	
LBrnDia (cm)	2.53	2.68	2.46	2.13	3.46	1.74	0.058 (R)
	(0.55)	(0.49)	(0.53)	(0.95)	(0.67)	(0.48)	(1, 2) (1–3)
MBrnDia (cm)	2.46	2.64	2.15	1.99	3.22	1.61	0.050 (R)
	(0.67)	(0.54)	(0.55)	(0.41)	(1.17)	(0.52)	(1, 2) (1–3)
UBrnDia (cm)	1.75	1.79	1.61	1.60	1.98	1.15	ns (R)
	(0.46)	(0.58)	(0.34)	(0.66)	(0.70)	(0.41)	
LBrnAng (degrees)	57.6	73.0	61.8	65.6	52.7	60.7	0.043
	(9.00)	(10.7)	(13.2)	(12.0)	(5.70)	(9.00)	(1, 2) (2, 3)
MBrnAng (degrees)	54.3	60.8	61.4	60.0	49.5	54.5	0.029
	(18.8)	(10.7)	(9.00)	(9.70)	(10.0)	(12.1)	(1, 2) (1–3)
UBrnAng (degrees)	47.5	56.5	52.7	49.2	46.3	50.2	ns
	(9.80)	(10.7)	(8.10)	(8.40)	(9.70)	(10.4)	

[a] DisSwp, distance from the tree base to the start of the bole sweep; DisCrk1, distance from the tree base to the first crook; CrnLen, crown length; LCrnDia, MCrnDia, UCrnDia, crown diameter at 2, 4, and 6 m, respectively; CrnDens, crown density as a percent of total crown volume occupied by foliage; CrnRR, crown recession rate; LBrnNum, MBrnNum, UBrnNum, branch number at 2, 4, and 6 m, respectively; LBrnLen, MBrnLen, UBrnLen, average branch length at 2, 4, and 6 m, respectively; LBrnDia, MBrnDia, UBrnDia, average branch diameter at 2, 4, and 6 m, respectively; LBrnAng, MBrnAng, UBrnAng, average branch angle at 2, 4, and 6 m, respectively.

[b] Values in parentheses represent 1 SD.

[c] Results of least significant difference comparisons following one-way ANOVA of good, average, and poor groups. Significant probability levels are presented as well as the stand quality groupings: 1, good; 2, average; and 3, poor. Quality groupings contained within parentheses are not significantly different from each other. Variables indicated with "R" were analyzed as studentized residuals of their regressions on tree height.

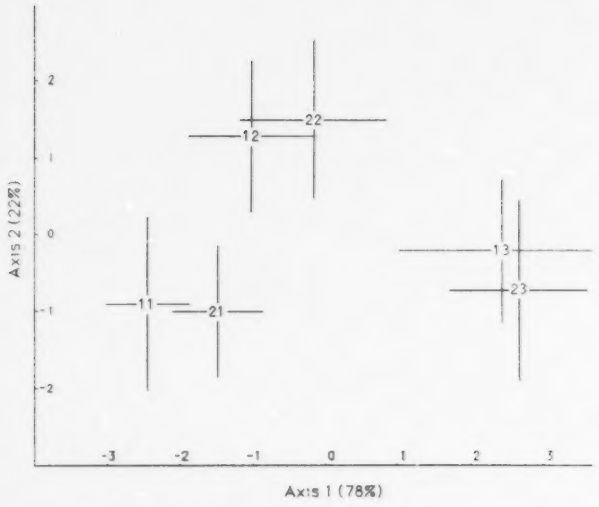

FIG. 2. Two-dimensional ordination between good-, average-, and poor-quality jack pine stands using canonical discriminant analysis. Horizontal and vertical lines represent 1 SD to each side of site means.

maintains this magnitude in its coefficient (–0.941) in the second canonical function (Table 3). Of the stem variables highly significant in the univariate ANOVA (Table 2: crooks, taper, and shape), only shape made a relatively small contribution to either canonical function.

For the six crown variables, crown recession rate is the dominant factor in both canonical functions, with coefficients over 1.000 (Table 3). This result probably explains why crown recession rate is the only variable demonstrating significant differences between the three quality classes (Table 2). Lower crown diameter also has a large coefficient in the first canonical function (–0.889), whereas crown length becomes more important in the second canonical function (0.711). Although both crown length and crown recession rate were highly significant in the univariate ANOVA (Table 2), lower crown diameter was not significant.

None of the 12 branch variables proved to be extremely important in the first canonical function. The largest coefficient was associated with lower branch length (0.575), with three coefficients lower than 0.100 (Table 3). However, upper branch diameter (1.036) and middle branch angle (1.004) have the largest coefficients of all 24 variables in the second canonical function. Other variables such as upper branch number, middle branch length, middle branch diameter, and upper branch angle also provide important contributions to the second canonical function.

A large percent of individuals (88.3%) were correctly reclassified into their quality classes (Table 3) using the derived discriminant function. This result suggests that stand quality can be quantified from measures of stem, crown, and branch traits of randomly selected dominant trees within a given stand.

Simple and multiple linear regression

From the results of the simple linear regression, all three environmental forces, namely competition, microsite, and climate, proved to be important in determining form (Table 4). Total basal area ($r^2 = 0.420$, $p = 0.000$), soil moisture regime ($r^2 = 0.225$, $p = 0.000$), number of frost-free days ($r^2 = 0.140$, $p = 0.003$), and total annual precipitation ($r^2 = 0.228$, $p = 0.000$) all had highly significant results when regressed on the first canonical axis. Only soil moisture regime was highly significant ($r^2 = 0.197$, $p = 0.000$) when regressed on the second canonical axis.

TABLE 3. Results of canonical discriminant analysis of form variables for good-, average-, and poor-quality stands of jack pine

Variable[a]	Standardized canonical function coefficient: Canonical function 1	Canonical function 2
Sweep	0.336	0.207
DisSwp	0.108	–0.146
Crooks	1.036	–0.599
DisCrk1	0.442	–0.006
Taper	0.927	–0.941
Shape	0.064	–0.362
CrnLen	0.326	0.711
LCrnDia	–0.889	0.530
MCrnDia	0.095	–0.271
UCrnDia	–0.013	–0.180
CrnDens	–0.085	–0.181
CrnRR	1.109	1.004
LBrnNum	0.251	–0.154
MBrnNum	–0.042	0.139
UBrnNum	–0.045	0.601
LBrnLen	0.575	0.416
MBrnLen	–0.323	–0.883
UBrnLen	–0.271	–0.576
LBrnDia	0.496	–0.085
MBrnDia	–0.087	0.620
UBrnDia	0.277	1.036
LBrnAng	0.310	0.044
MBrnAng	0.146	1.004
UBrnAng	–0.508	–0.761
Cumulative variance (%)	78.2	100.0
Trees correctly reclassified (%)	88.3	

[a] Variable abbreviations are defined in Table 2.

The nonclimatic environmental variables, when combined in a multiple linear regression, explained 55.7% (first canonical function) and 35.1% (second canonical function) of the variation in tree form (Table 4). Soil moisture index was present in both regression models, along with different expressions of competition and microsite.

Discussion

Ideally, all stands chosen for a study comparing form on a stand basis should have the same average height, be even-aged and of fire origin, be located on sites with equivalent site quality, and have uniform local environments. These conditions were impracticable, if not impossible, to attain for this study, so we compensated by removing the effect of size by treating height as a covariate for comparisons based on size-affected variables. Technically, jack pine height growth over time on better sites is a curvilinear function (Wiltshire 1982; Lenthall 1986), and our sample stands were of different ages. Since the poor-quality stands were the youngest and the good-quality stands were the oldest, departures from linearity in height growth over time would tend to emphasize this difference. Thus, our procedure based on simple linear regression may not have removed all of the size-related variation.

TABLE 4. Results of simple and multiple linear regression of canonical functions expressing form against environmental variables for good-, average-, and poor-quality stands of jack pine

	y-variables			
	Canonical function 1		Canonical function 2	
x-variable	r^2	*p*	r^2	*p*
Simple regression				
Competition				
Total basal area	0.420	0.000**	0.002	0.760
Competition index	0.009	0.462	0.057	0.066
Density	0.011	0.436	0.000	0.994
% opening	0.012	0.411	0.037	0.143
Microsite				
Depth LFH	0.067	0.046*	0.009	0.481
Depth A	0.038	0.138	0.048	0.091
Depth B	0.090	0.020*	0.000	0.879
Depth BC	0.053	0.076	0.000	0.924
% coarse A	0.019	0.219	0.004	0.645
% coarse B	0.018	0.310	0.001	0.858
% coarse BC	0.019	0.300	0.012	0.406
% coarse C	0.015	0.354	0.002	0.772
Soil moisture index	0.225	0.000**	0.197	0.000**
Soil drainage index	0.088	0.021*	0.058	0.064
Slope	0.047	0.095	0.044	0.108
Climate				
Frost-free days	0.140	0.003**	0.021	0.264
Jan. temp.	0.096	0.016*	0.081	0.028*
July temp.	0.026	0.219	0.030	0.190
Precipitation				
Snow	0.001	0.842	0.004	0.614
Total	0.228	0.000**	0.003	0.671
Growing degree-days	0.104	0.012*	0.018	0.313
Elevation	0.003	0.665	0.002	0.717
Multiple regression				
	0.557	0.000**	0.351	0.000**
x-variables[a]	Total basal area, competition index, density, depth LFH, % coarse BC, soil moisture		% opening, depth A, soil moisture	

NOTE: Significance levels less than 0.05 are superscripted with a single asterisk, and levels less than 0.01 are superscripted with a double asterisk.

[a]The six climatic variables and elevation were not included in the multiple regressions.

Traits contributing to good form in jack pine

Evaluation of form in jack pine and other conifers is actually a judgement based on a summation of numerous stem, crown, and branch characters. In this study, comparisons of natural stands subjectively rated as good, average or poor based on quantitative and multistate variables indicated that significant differences were expressed for half of the chosen 24 variables in each of the three categories. While we were interested in the variables that showed the greatest differences between stand quality classes, the variables that did not show significant differences are also of interest since the stands were chosen to represent examples of the extremes, as well as average examples, of form.

For variables that did not show significant differences between quality classes, trends from good to poor were still evident for the stem variables sweep, distance to sweep, and distance to the first crook (Table 2), but too much overlap existed for the differences to be significant. Perhaps more extensive sampling would demonstrate significant differences for these stem traits as well. No significant differences nor obvious trends existed for crown diameter and branch lengths at the three crown sampling points, indicating that the more compact crowns of the good-quality stands were the result of relatively shorter crowns and not smaller diameter crowns. Crown diameters and branch lengths are closely related traits that seem to be a function of stand density (Table 1), reflecting the growing space available to the sampled trees. Thus, it is of particular interest that these traits do not show more pronounced differences between sampled stands since form in jack pine is thought to be largely a function of spacing.

The results of this study demonstrated that the differences that separate a poor-quality stand from an average stand are more pronounced than those separating good from average stands. In most cases where significant differences were

expressed between quality classes, good and average stand types were not significantly different (Table 2). This trend was evident within each of the three categories of form traits.

Similarly, the discriminant analysis showed that the poor-quality stands were considerably more distinct from the other two types on the first, or main, axis of variation (Fig. 2). The second axis, an orthogonal component of variation, was necessary to cleanly separate the two average stands from the two good stands (Fig. 2), meaning that differences are expressed not just in degree but also in kind among the three stand quality categories. Thus, the variables making the greatest contribution to the first canonical function, which are primarily stem and crown characters, are most important for distinguishing the poor-quality stands from the others. Conversely, all four types of branch traits (number, length, diameter, and angle) as well as stem and crown traits contributed strongly to the separation of average from good stands on the second canonical axis. These results indicate that pronounced differences resulting in poor form in jack pine stands from both west and east of Lake Nipigon in Ontario result from differences in stem and crown form traits rather than branch traits.

The variable crown recession rate was the best descriptor of form of the 24 variables measured for this study. Even so, owing to the uneven ages and different heights of the three stand quality groups, the results for this variable are confounded. The best quality stands have the shortest crowns relative to height and they also have the lowest crown recession rates. However, these rates were determined as average values at 2, 4, and 6 m below the base of the crowns of trees whose height growth had begun to slow, and presumably the rates would have been much higher had they been determined nearer the ground. Stand comparisons based on this variable at a fixed age would have been more desirable, but would have involved a much more intensive experimental procedure.

Factors determining form in jack pine

Extremely shallow soils, spacing, and genetics are three factors thought to play a role in determining form in jack pine. In this study the first factor can be disregarded since all sampled stands were located on deep soils. There is a strong possibility that genetic differences may play a determinant role. Not all of the form variation expressed on the two canonical axes could be explained by environmental factors; thus, genetic differences likely account for some of this variation. However, the role that genetic differentiation plays in determining form differences among and within the six stands must await the results of progeny testing begun in the spring of 1990. A short-term field trial has been established as a test of wind-pollinated progenies from our 60 parent trees, as well as 20 plus-tree families, grown under different initial spacings (ranging from 0.25 to 3.00 m) in a common plot on two contrasting sites. This trial will be used to determine (*i*) narrow-sense heritabilities and genetic correlations of the traits that determine jack pine form and (*ii*) changes to these parameters at the different spacings. For example, we would like to verify that the genetic component becomes increasingly important at wider spacings, to determine whether the relative importance of this component varies with site quality, and to determine whether its relative importance changes over time.

Four of the six regressions of interpolated climatic data against the first canonical variate axis scores were significant, and one was significant against the second axis scores (Table 4). Total precipitation explained 22.8% of the variation expressed on the first axis, and this result seems to coincide well with the strong correlations with soil moisture, which are discussed below. However, except for one variable, number of frost-free days, there were minimal climatic differences with no apparent trends among stands, making the regression results difficult to interpret. The considerable variation existing in number of frost-free days gives some indication that the best form is associated with a greater number of frost-free days, although one poor-quality stand has a comparably long frost-free period. A correspondence of poor form with damaging frosts is logical in that frost damage can lead to misshapen growth. At the same time it is puzzling since jack pine is frost hardy, and visible damage that can be readily attributed to this source is absent or very uncommon in natural stands from the study area.

Since spacing is thought to play a key role in determining the form of jack pine, we expected that the four competition variables measured for this study would explain more of the form-related variation as independent variables in simple and multiple linear regressions against the two canonical variate axes (Table 4). For example, an earlier study showed that available growing space for young jack pine seedlings was effectively determined by the use of hemispherical photographs (MacDonald *et al.* 1990). However, the camera focal plane was situated in close proximity to the developing canopy of the young stand. In contrast, the camera location in our study was approximately 6–7 m below the base of the crowns. This distance factor may have distorted the "effective" canopy opening and could, therefore, account for the poor correlation between percent opening and the two canonical variate axes.

Only one of the four competition variables, basal area, explained a large component of variation (42%) in the simple linear regression against the first canonical variate axis; and none of the four produced significant simple regressions against the second axis (Table 4). Intuitively, this result suggests that form in jack pine does depend on level of competition and that a simple basal area determination by prism sweep gives a better indication of effective competition than the other three variables. While there is support for this generalization from earlier work (Van Damme and Parker 1987), examination of the data reveals that stand age may be a confounding factor. Basal area in the stands corresponds approximately to stand age, and the poor-quality stands having the lowest basal areas are the youngest and third youngest of the six stands.

In contrast with the results of simple regressions, the results of the multiple regressions explaining 55.7 and 35.1% of the variation expressed on the first and second canonical variate axes emphasize the importance of all four competition variables. Basal area, competition index, and density, as measured, remained in the regression against the first axis, and percent opening remained for the second axis. Perhaps the reason the competition variables are not better indicators of stand form in the simple regressions is that the present-day form was determined in the early stages after stand establishment, when spacings were much tighter. Subsequent mortality has increased the spacing between trees, with the possible result that differences in present-day stand densities have become less pronounced.

The most surprising aspect of our results is that soil moisture and climatic variables explained significant components of form variation in jack pine. Soil moisture index was the

only environmental variable that was significant in simple regressions against both axes, explaining 22.5 and 19.7% of the variation expressed on the first and second axes, respectively (Table 4). This variable was also retained in both multiple regressions. The related variable soil drainage index also explained a significant component of first-axis variation. The pattern that emerges from these results is that soils producing higher levels of moisture stress are associated with the better quality stands in this study. This pattern is the opposite of what we would predict, since jack pine growing on very thin soils is stunted with poor form (Hosie 1969), presumably as a result of severe moisture stress. Zimmermann and Brown (1971) also noted that trees growing under moisture stress (e.g., semiarid regions, locally severe sites) exhibited a shrubby appearance due to reduced growth and early loss of apical control. Thus, the effect that moisture stress has on the form of jack pine apparently depends on soil depth.

One possible explanation for the association of better form with greater moisture stress on deep soils is related to the type of competition and the resulting mortality rate at the time of stand establishment. Newly established jack pine trees face greater levels of competition from other conifer and flowering plant species on soils with less moisture stress. On these sites, the competing species quickly overtop the pine, forming a dense canopy which, in turn, severely limits the amount of photosynthetically active radiation available to the jack pine seedlings (Morris *et al.* 1990). Under this condition of low light, mortality would be extremely high for the shade-intolerant jack pine seedlings. Once the surviving seedlings emerge from the competing canopy, additional mortality would be low on these water- and nutrient-rich sites, but intertree distances between individual jack pine trees could be quite large, causing individuals to exhibit poor form. On the drier sites, competition is largely intraspecific (Fowells 1965). Light availability initially is not a limiting factor on these sites (Kenkel 1988), giving rise to higher stand densities of jack pine in the early stage of establishment. Crown closure would be accomplished rapidly, reducing the available growing space for individuals. On these water- and nutrient-poor sites, mortality would increase after crown closure, but the effect of the initial limitation of growing space would lead to better form in the emerging dominant trees.

A simpler explanation, but not necessarily an alternative, is that moisture stress leads to more intense competition, which modifies the form of jack pine trees with or without the presence of other species. Earlier work has shown that water availability may be the single most important limiting factor in natural jack pine stands growing on sandy soils. Yarranton and Yarranton (1975) noted that mortality of the weaker suppressed trees coincided with years having summer droughts. Thus, the association of water stress with better form noted here likely is connected to higher levels of intraspecific competition. Perhaps, competition for moisture tends to regulate form as a factor superimposed upon competition for light and space, although it certainly is possible that the two are sequential; mortality from moisture stress determines growing space and light availability.

While it is not clear how climatic and soil moisture factors affect the form of mature jack pine stands, our results may open a Pandora's box for the forest manager. Without passing judgement on the importance of genetics, it may not be possible to arrive at a final density optimizing tree form by selecting a single optimum spacing for planting or a single thinning schedule. Owing to the coarse nature of the soils where jack pine predominates, climatic circumstance and soil factors determining available moisture modulate the actual intensity of intraspecific competition depending on initial spacing and subsequent stand densities, as well as spatial patterns. This influence, in turn, affects levels of suppression, self-pruning, rates of self-thinning, and apparently the various traits associated with crown and stem form that are the focus of this study.

A need exists to determine the role that moisture stress plays in determining jack pine form and, hence, value. While the influence of climate will be difficult to determine in field experiments, additional insight can be attained by monitoring form of jack pine spacing trials established on sites with varying levels of moisture stress and competition trials involving various levels of interspecific competition.

Conclusions

Pronounced differences resulting in poor form for our jack pine stands resulted from differences in stem and crown form traits rather than branch traits. Branch characters made an important contribution in distinguishing differences between the average- and good-quality stands.

Soils producing higher levels of moisture stress are associated with better quality stands in this study. It is suggested that perhaps competition for moisture regulates form as a factor superimposed upon competition for light and space. This hypothesis regarding the regulatory function of moisture stress on form in jack pine requires additional research for verification.

Although identified as a potential contributor to form, the role that genetics plays in determining form must be determined from progeny tests currently being conducted.

Acknowledgements

The authors greatly appreciate the thorough and constructive reviews by Dr. George Buchert, Dr. Dennis Joyce, Ken Armson, and Dave Weingartner.

Atchley, W.R., Gaskins, C.T., and Anderson, D. 1976. Statistical properties of ratios. I. Empirical results. Syst. Zool. **25**: 137–148.

Bella, I.E., and DeFranceschi, J.P. 1974. Analysis of jack pine thinning experiments, Manitoba and Saskatchewan. Can. For. Serv. Publ. 1338.

Bella, I.E., and DeFranceschi, J.P. 1980. Spacing effects 15 years after planting three conifers in Manitoba. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-223.

Environmental Systems Research Institute. 1987. ARC/INFO. Vol. 1. User's guide. Environmental Systems Research Institute, Redlands, CA.

Environment Canada. 1982*a*. Canadian climate normals: temperature and precipitation 1951–1980 for Ontario. Environment Canada, Ottawa.

Environment Canada. 1982*b*. Canadian climate normals. Vol 4. Degree days 1951–1980. Environment Canada.

Forslund, R.R. 1991. The power function as a simple stem profile examination tool. Can. J. For. Res. **21**: 193–198.

Fowells, H.A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. Agric. Handb. 271.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hosie, R.C. 1969. Native trees of Canada. 7th ed. Canadian Forestry Service, Ottawa.

Janas, P.S., and Brand, D.G. 1988. Comparative growth and development of planted and natural stands of jack pine. For. Chron. **64**: 320–328.

Kenkel, N.C. 1986. Structure and dynamics of jack pine stands near Elk Lake, Ontario: a multivariate approach. Can. J. Bot. **64**: 486–497.

Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology, **69**: 1017–1024.

Lenthall, D.J. 1986. Height growth and site index of jack pine (*Pinus banksiana* Lamb.) in the Thunder Bay area: a system of site quality evaluation. M.Sc.F. thesis, Lakehead University, Thunder Bay, Ont.

MacDonald, G.B., Morris, D.M., and Marshall, P.L. 1990. Assessing components of competition indices for young boreal plantations. Can. J. For. Res. **20**: 1060–1068.

Magnussen, S., and Yeatman, C.W. 1987. Early testing of jack pine. II. Variance and repeatability of stem and branch characters. Can. J. For. Res. **17**: 460–465.

Maguire, D.A., and Hann, D.W. 1988. A stem dissection technique for dating branch mortality and reconstructing past crown recession. For. Sci. **33**: 858–871.

Maley, M.L. 1990. Phenotypic variation in cone and needle characters of *Pinus banksiana* Lamb. (jack pine) in northwestern Ontario. M.Sc.F. thesis, Lakehead University, Thunder Bay, Ont.

Morgenstern, E.K., Holst, M.J., Teich, A.H., and Yeatman, C.W. 1975. Plus- tree selection: review and outlook. Can. For. Serv. Publ. 1347.

Morris, D.M., MacDonald, G.B., and McClain, K.M. 1990. Evaluation of morphological attributes as response variables to perennial competition for four-year-old black spruce and jack pine seedlings. Can. J. For. Res. **20**: 1696–1703.

Ontario Institute of Pedology. 1985. Field manual for describing soils. 3rd ed. Ontario Institute of Pedology, Guelph.

Ontario Ministry of Natural Resources. 1987. Tree improvement master plan for Ontario. Queen's Printer, Toronto.

Ontario Ministry of Natural Resources. 1990. Summary of timber harvested on crown lands by species. Ontario Ministry of Natural Resources, Forest Management Branch, Forest Resources Group, Sault Ste. Marie, Ont.

Rudolph, T.D., and Yeatman, C.W. 1982. Genetics of jack pine. U.S. For. Serv. Wash. Off. Res. Pap. WO-38.

Schoenike, R.E. 1976. Geographical variations in jack pine (*Pinus banksiana* Lamb.) Tech. Bull. Univ. Minn. Agric. Exp. Stn. For. Ser. 21: 304–1976.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman, San Francisco.

Timell, T.E. 1986. Compression wood in gymnosperms. Vol. 2. Springer-Verlag, New York.

Van Damme, L., and Parker, W.H. 1987. Selection of *Picea mariana* for growing space efficiency. Can. J. For. Res. **17**: 421–427.

Whitney, R.D., and McClain, K.M. (*editors*). 1981. Boreal Mixedwood Symposium. Can. For. Serv. Great Lakes For. Cent. COJFRC Symp. Proc. O-P-9.

Wiltshire, W.B. 1982. Polymorphic site index curves for jack pine in the Thunder Bay Region. B.Sc.F. thesis, Lakehead University, Thunder Bay, Ont.

Yarranton, M., and Yarranton, G.A. 1975. Demography of a jack pine stand. Can. J. Bot. **53**: 310–313.

Zimmermann, M.H., and Brown, C.L. 1971. Trees: structure and function. Springer-Verlag, New York.

Zobel, B.J., and van Buijtenen, J.P. 1989. Wood variation: its causes and controls. Springer-Verlag, New York.